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Above- and belowground carbon stocks are decoupled in secondary tropical forests and are positively related to forest age and soil nutrients respectively

RUNNING TITLE

Decoupled secondary tropical forest carbon stocks

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KEYWORDS

Aboveground biomass; Belowground biomass; Carbon storage; Forest restoration; Land-use change; Necromass; Neotropics; Soil; Succession

ABSTRACT

Reducing atmospheric CO2 is an international priority. One way to assist stabilising and reducing CO2 is to promote secondary tropical forest regrowth on abandoned agricultural land. However, relationships between above- and belowground carbon stocks with secondary forest age and specific soil nutrients remain unclear. Current global estimates for CO2 uptake and sequestration in secondary tropical forests focus on aboveground biomass and are parameterised using relatively coarse metrics of soil fertility. Here, we estimate total carbon stocks across a chronosequence of regenerating secondary forest stands (40–120 years old) in Panama, and assess the relationships between both above- and belowground carbon stocks with stand age and specific soil nutrients. We estimated carbon stocks in aboveground biomass, necromass, root biomass, and soil. We found that the two largest carbon pools - aboveground biomass and soil – have distinct relationships with stand age and soil fertility. Aboveground biomass contained ~61-97 Mg C ha-1 (24-39 % total carbon stocks) and significantly increased with stand age, but showed no relationship with soil nutrients. Soil carbon stocks contained ~128-206 Mg C ha-1 (52-70 % total stocks) and were unrelated to stand age, but were positively related to soil nitrogen. Root biomass carbon stocks tracked patterns exhibited by aboveground biomass. Necromass carbon stocks did not increase with stand age, but stocks were held in larger pieces of deadwood in older stands. Comparing our estimates to published data from younger and older secondary forests in the surrounding landscape, we show that soil carbon recovers within 40 years of forest regeneration, but aboveground biomass carbon stocks continue to increase past 100 years. Above- and belowground carbon stocks appear to be decoupled in secondary tropical forests. Paired measures of above- and belowground carbon stocks are necessary to reduce uncertainty in large-scale models of atmospheric CO2 uptake and storage by secondary forests.

1. INTRODUCTION

Tropical forests are a persistent sink of atmospheric CO_2 and store 55 % of global terrestrial carbon, estimated at 471 $\pm$ 93 petagrams (Pg; Pan et al., 2011). In an era of unprecedented anthropogenic greenhouse gas emissions resulting in pervasive changes in global climatic patterns, maintaining tropical forest cover is key to stabilising the global carbon balance (Grace, Mitchard, & Gloor, 2014;

55 Yadvinder Malhi & Grace, 2000). Deforestation and conversion to agriculture removes aboveground
56 biomass, shifts plant composition and function, and alters soil nutrient levels and local precipitation
57 (Dent, DeWalt, & Denslow, 2013; Grace et al., 2014). Such changes drive increased carbon turnover
58 and emissions estimated at 1-2 petagrams of carbon per year (Pg C $year^{-1}$; Houghton, Byers, &
59 Nassikas, 2015; Pan et al., 2011).
60
61 Approximately 50 % of global tropical forest cover is now degraded or regenerating secondary forest,
62 rather than old-growth forest (FAO, 2016). Secondary forests are therefore increasingly important for
63 the provision of tropical forest ecosystem services, such as uptake of atmospheric CO_2 and long-term
64 carbon storage (Chazdon et al., 2016). Recent pan-tropical analyses have shown that aboveground
65 biomass and carbon stocks of regenerating secondary tropical forests accumulate to 34.53 $\pm$ 1.84 Mg
66 C ha^{-1} by 20 years of regrowth, rising to 133.89 $\pm$ 4.67 Mg C ha^{-1} by 100 years of regrowth
67 (Anderson-Teixeira, Wang, McGarvey, & LeBauer, 2016). This rapid accumulation of carbon
68 represents an estimated net carbon sink of ~1-3 Pg C $year^{-1}$ (Houghton et al., 2015; Pan et al., 2011).
69
70 In the Neotropics, regenerating secondary forests (1-100 years old) take up CO_2 at 11 times the rate of
71 old-growth forests, and during the first 20 years of secondary forest regeneration the rate of uptake is
72 3.05 Mg C ha^{-1} $year^{-1}$ (Poorter et al., 2016). Indeed, the total accumulation of carbon over 40 years of
73 secondary forest regrowth on former agricultural land in tropical Latin America is equivalent to ~20
74 years (1993 – 2014) of carbon emissions from fossil fuels and industrial processes across the region
75 (Chazdon et al., 2016). The preservation of intact old-growth tropical forests and existing secondary
76 forests, alongside the promotion of secondary forest regrowth on abandoned land, could therefore
77 constitute a powerful tool in policies aimed at mitigating climate change such as the Bonn Challenge
78 and REDD+ (Berenguer et al., 2014; Chazdon et al., 2016).
79
80 The quantity of carbon stored within tropical forests is determined by feedbacks between plant net
81 primary production (NPP), soil fertility and climate. At regional scales, NPP of old-growth and

secondary tropical forests increases with precipitation and soil fertility (Anderson-Teixeira et al., 2016; Malhi et al., 2004; Malhi et al., 2009; Poorter et al., 2016). The spatial heterogeneity of available soil nutrients (such as nitrogen, phosphorus and potassium; Wright et al., 2011), topography (Grimm, Behrens, Märker, & Elsenbeer, 2008), and plant composition (Batterman et al., 2013; Jobbagy & Jackson, 2000) can be important determinants of forest carbon stocks at finer spatial scales.

Considerable uncertainty surrounds the relationship between carbon stocks in different carbon pools and secondary forest stand age; although above-ground biomass tends to increase over succession, field studies report increases, decreases and unchanged soil carbon over similar time-scales (reviewed in Powers & Marín-Spiotta (2017)). Current large-scale estimates of carbon uptake and stocks in secondary forests often consider only aboveground biomass (Poorter et al., 2016) or soil carbon (Don, Schumacher, & Freibauer, 2011), and rarely include multiple above- and belowground carbon pools (but see Anderson-Teixeira et al. (2016)). Considering both above- and belowground carbon stocks in concert is essential to understand how total forest carbon accumulates as forests regenerate, particularly when planning forest conservation policies aimed at promoting carbon uptake and sequestration (Chazdon et al., 2016; Powers & Marín-Spiotta, 2017). Furthermore, present estimates of the importance of soil nutrients in determining aboveground carbon stock accumulation are based on soil cation exchange capacity (CEC; Poorter et al. (2016)). Soil CEC can be a relatively coarse metric of soil fertility if site-specific values are unavailable (Nachtergaele, van Velthuizen, Verelst, & Wiberg, 2012). Therefore, we may be underestimating the importance of specific soil nutrients, such as N and P, in determining secondary forest above- and belowground carbon stock accumulation (Powers & Marín-Spiotta, 2017).

To better understand how regenerating secondary forests may contribute to reducing atmospheric CO_2 through carbon uptake and long-term sequestration, we urgently need more detailed understanding of the process of carbon accumulation and the relative importance of different carbon pools as secondary

forests develop (Chazdon et al., 2016). Specifically, we need to measure above- and belowground carbon stock estimates with plot-level data for targeted soil nutrients (Powers & Marín-Spiotta, 2017). Additionally, our knowledge of carbon stocks in intermediate (~60-90 years) and older (>100 years) secondary forests is limited (Anderson-Teixeira et al., 2016). Such information is vital to enhance predictive power regarding the long-term value of secondary forests in strategies to mitigate climate change (Chazdon et al., 2016), while contextualising the exceptional value of maintaining intact primary tropical forests and their existing carbon stocks (Grace et al., 2014).

The aim of our study was to assess the effect of forest stand age and specific soil nutrients on carbon storage within different secondary tropical forest carbon pools. We use a chronosequence in central Panama – which has the unique advantage of consistent rainfall and pH across sites and spans the longest trajectory of secondary forest regeneration in the Neotropics (40 – 120 years; Rozendaal et al., 2019) – to estimate carbon stocks in above- and belowground biomass and necromass. Specifically, we ask 1) do all carbon pools increase consistently with forest age? And 2) what is the relative importance of forest age and soil nutrients for carbon stock accumulation in different carbon pools? Answers to these questions will further elucidate patterns of total carbon accumulation over secondary forest regeneration and how they vary among different above- and belowground carbon pools. Furthermore, we will be better able to demonstrate the role specific soil nutrients play in carbon accumulation in regenerating tropical forests. Parameterising large-scale models of carbon uptake and storage within regenerating secondary tropical forests is key to demonstrating the importance of secondary forests in national and international carbon mitigation strategies and forest restoration goals (Chazdon et al., 2016).

2. MATERIALS AND METHODS

2.1 Study area

This study was conducted across a 40–120 year secondary forest chronosequence located in central Panama within the Barro Colorado Nature Monument (BCNM) and includes sites on Barro Colorado

Island (BCI; 9°9′ N, 79°51′ W) and nearby mainland peninsulas (Fig. 1; Denslow & Guzman, 2000). The BCNM comprises a mosaic of old-growth and secondary tropical forests of different ages, which are the product of forest regrowth following successive episodes of agricultural land abandonment between the 1880s and 1979 (Denslow & Guzman, 2000; E. G. J. Leigh, Rand, & Windsor, 1982). We define old-growth stands as those with no indication of historical logging or cultivation (Piperno, 1990). The region receives ~2600 mm of rainfall annually, predominantly during a 7-month wet season from May to December (Leigh et al., 1982). Geologically, the BCNM is a patchwork of volcanic and sedimentary parent material that has weathered to form clay-rich oxisols and silty-clay alfisols (Baillie, Elsenbeer, Barthold, Grimm, & Stallard, 2007; Yavitt, 2000).

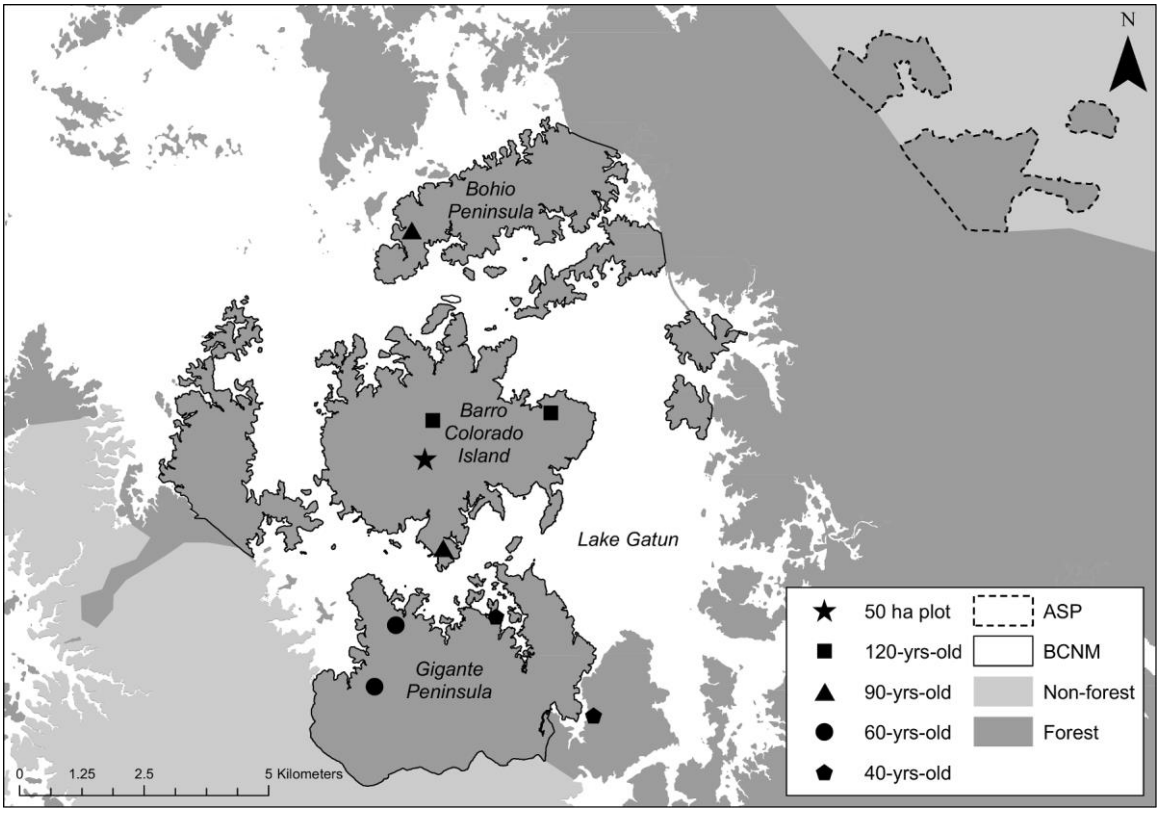


Fig. 1: Geography of the eight 1-ha chronosequence study plots within the Barro Colorado Nature Monument (BCNM), Panama. Chronosequence forest stands span 40-120 years of forest regeneration since agricultural land abandonment. The Barro Colorado Island (BCI) 50-ha plot comprises old-growth forest. ASP = Agua Salud Project, which comprises secondary

forest stands 5 to 15 years old. Map modified from Mayhew, Tobias, Bunnefeld, & Dent (2019).

2.2 Chronosequence plots

All data were collected within a network of eight permanent secondary forest plots representing two independent replicate 1-ha plots (50 x 200 m) in each of 40, 60, 90 and 120-year-old secondary forest stands (Fig 1; see Denslow & Guzman, 2000 and Dent et al., 2013 for further details). Stand ages were estimated using historical records, aerial photographs and interviews with long-time residents (for details see Denslow & Guzman 2000). Stands selected for plot establishment were a minimum of 1.3 km apart (mean ± SD = 4.65 ± 2.28 km), were previously small-holdings farmed for fruit production and/or cattle pasture, and have not been subjected to further disturbance since land abandonment. Plots are located on different geological substrates but have similar values for soil pH and bulk density (see Denslow & Guzman (2000) for detailed plot characteristics). Due to limitations imposed by the landscape composition and land-use history, secondary forest plot age was closely linked with geology: all younger plots (aged 40 and 60 years) were exclusively associated with basaltic substrates, and older plots (aged 90 to 120 years) were associated with sedimentary substrates (Denslow & Guzman, 2000).

2.3 Carbon pool data collection and calculation

All trees and palms ≥10 cm diameter at breast height (DBH) were measured for diameter and identified to species-level between 2011 and 2014, following census protocols established by the Forest Global Earth Observatory (ForestGEO; Condit, 2008). Soil sampling and necromass inventories were undertaken between February and May 2015, following protocols established for the ForestGEO 50-ha plot on BCI (Larjavaara & Muller-Landau, 2009; Turner, 2010).

Above- and belowground biomass and community-weighted mean wood density

We followed methods in Poorter et al. (2016) for estimating aboveground biomass for all trees and palms from diameter data and species-specific wood density values, compiled for trees and palms in

177 the BCNM (Wright et al., 2010). If a species-specific wood density value was not available for an
178 individual, we used the genus-level mean wood density. We estimated the aboveground biomass of
179 each individual using the allometric equation developed by Chave et al. (2014; equation 7, which
180 incorporates a constant specific to temperature and water stress of the study area). Lack of height data
181 precluded our use of a palm-specific allometric equation (Goodman et al., 2013). It was not feasible to
182 physically remove any large tree roots from plots in order to estimate belowground root biomass, due
183 to the consequential impacts to trees and long-term aboveground biomass monitoring. Thus, we
184 estimated root biomass for each individual from DBH and wood density values using an allometric
185 equation developed within Panamanian secondary forests (Sinacore et al., 2017). To obtain carbon
186 stock estimates from above- and belowground biomass estimates, we assumed 47.4 % of biomass to
187 be carbon and so multiplied biomass estimates by 0.474 (Martin & Thomas, 2011). We depart from
188 the methods of Poorter et al. (2016) by using 47.4 % rather than 50 %, because the values of Martin &
189 Thomas (2011) were tested in the BCNM, increasing our confidence in this value. Our aboveground
190 biomass carbon stock calculations will therefore be lower than Poorter et al. (2016). For each plot, we
191 generated a per-hectare estimate of total carbon stocks (Mg C ha^{-1}) for the aboveground and root
192 biomass carbon pools, by summing the estimated carbon stocks held in each individual. We also
193 generated plot-level estimates for total basal area (m^2) from DBH measurements, and we calculated
194 plot-level community-weighted mean wood density by summing wood density values across all
195 individuals and dividing by the number of individuals.
196
197 *Necromass*
198 Fallen dead wood (≥10 cm diameter) was inventoried along 1000 m of parallel transects located
199 within each 1-ha plot (5 x 200 m transects, spaced at 10 m intervals) using the line-intercept method
200 (Larjavaara & Muller-Landau, 2009). The diameter of all deadwood bisecting a transect was recorded,
201 along with its orientation (Larjavaara & Muller-Landau, 2011). All standing deadwood ≥10 cm
202 diameter (diameter at 1.3 m if ≥1.3 m high or diameter at the mid-point of the stump if <1.3 m high)
203 was inventoried throughout 1-ha plots, with diameter and height recorded. For fallen and standing

deadwood ≥20 cm diameter, we estimated wood density non-destructively using a penetrometer and a relationship developed for deadwood ≥20 cm diameter within the BCNM (Larjavaara & Muller-Landau, 2010). For deadwood <20 cm diameter, a plot-level mean wood density was used, derived from the ≥20 cm diameter deadwood. Carbon stocks within each piece of fallen necromass were summed for each transect, as was necromass abundance and volume (Larjavaara & Muller-Landau, 2011). Plot-level total necromass carbon stock estimates were generated by summing carbon stocks of individual pieces of standing and fallen deadwood.

Soil sampling

Within each 1-ha forest plot, soil samples were collected along two, parallel 200 m transects, spaced 30 m apart. Five sampling points were located at 40 m intervals along each transect, giving 10 sampling points per plot. Soil was collected from 0-10 cm and 10-20 cm at all 10 sampling points, while at alternate sampling points (n = 5) deeper soils from 20-50 cm and 50-100 cm were also collected. Sampling generated 30 samples per plot (0-10 cm, n = 10; 10-20 cm, n = 10; 20-50 cm, n = 5; and 50-100 cm, n = 5). If a sampling point was disturbed by animals (for example, tracks or burrows), sampling was carried out at the closest undisturbed area. Obvious surface litter, including decaying but recognisable leaves and twigs, was removed at the sampling point; any surface roots were left intact.

Soil cores from 0-10 cm and 10-20 cm depths were taken using a 2-inch-diameter, fixed-volume auger. If stones or roots interrupted coring, then the roots were cut or sampling was started again within 1.5 m of the original sampling point. The entire sample, including roots and stones, was taken back to the lab for processing. Soils from 20-50 cm and 50-100 cm depths were sampled using a Dutch auger. If coring was interrupted by stones and the depth achieved was <80 % of the required depth, sampling was started again within 1.5 m of the original sampling point. If the depth achieved was ≥80 % of the required depth, the exact depth achieved was recorded. Soil from each core was homogenised in the field, with a 500 g subsample taken back to the lab for processing.

231

232 For all soil samples, we removed all roots (>2mm diameter) and stones by hand, air-dried the soil in
233 an air-conditioned laboratory for a minimum of five days, and calculated sample-specific bulk
234 densities corrected for stone fraction (SI1). Due to the coring technique used for 20-50 cm and 50-100
235 cm cores, core-specific bulk density values could not be obtained. Instead, we used bulk density
236 values and estimated stone fraction from soil pits located close to each 1-ha plot (B. Turner pers.
237 comm; H. Elsenbeer pers. comm.).
238

239 Only soil cores that reached ≥80 % of the required depth were used for soil carbon analyses so as not
240 to bias the carbon and nutrient concentration data for each depth interval. Individual soil samples were
241 ground and analysed for percentage carbon and nitrogen using a CN analyser (Elementar Vario III
242 EL). Available phosphorus was extracted using 0.5M $NaHCO_3$ buffered at pH 8.5, and content
243 determined colorimetrically by the molybdenum blue method. Phosphorus data were only obtained for
244 0-10cm and 10-20cm soil depths. Soils within the chronosequence stands have relatively low pH (i.e.
245 <7); therefore, we did not expect carbonates to be present and assumed that carbon concentration
246 values were equivalent to soil organic carbon (Denslow & Guzman, 2000; Grimm et al., 2008). Soil
247 carbon stock estimates were generated by correcting percentage carbon values using soil bulk density
248 values for each sample (please see SI1 for full details). Estimates for soil carbon stocks, available
249 phosphorus, and percentage nitrogen at each soil depth, as well as totals for each in soil 0-100 cm
250 depth, were calculated using equations outlined in SI1.
251

252 2.4 Integrating carbon stock data from the surrounding landscape

253 Using published data, we compiled values of aboveground biomass carbon and soil carbon stocks
254 from secondary and old-growth forest sites within the surrounding landscape. The additional data
255 included sites with much younger secondary forests of 5 to 15 years regrowth in the Agua Salud
256 chronosequence (Neumann-Cosel, Zimmermann, Hall, van Breugel, & Elsenbeer, 2011) and old-

growth forests on BCI (Chave et al., 2003; Grimm et al., 2008; Fig. 1). Carbon stock data for necromass and root biomass have not been published for these other sites.

2.5 Data analyses

We used a combination of generalised linear (GLMs) and generalised linear mixed effects models (GLMMs) for analyses of each carbon pool using R (version 3.6.1; (R Core Team, 2019) and the 'glmmTMB' package (Magnusson et al., 2019). Predictor variables included in models, such as forest stand age and specific soil nutrients, varied depending on the response variable and relevance to the hypothesis being tested (Table S2.1). Prior to analysis, continuous predictor variables were rescaled (mean-centred and standardised by two standard deviations; Gelman & Su, 2016; Schielzeth, 2010) to enable direct comparison of effect sizes. The distribution of response variables was visually inspected and the appropriate distribution selected for models (Bolker, 2008); Table S2.1).

For each response variable, the potential co-linearity of predictor variables was assessed using a Pearson's correlation matrix, with significant correlation taken as $r > 0.7$ ($P < 0.05$). Belowground root biomass was estimated from aboveground biomass and therefore these variables were not included together as predictor variables in analyses. Prior 'land use' and 'substrate geology' were both fitted as random effects to account for potential variation arising from these plot-level characteristics (Bolker et al., 2009).

Models were simplified by comparing AICc values using the R package 'MuMin' (Barton, 2017), whereby a difference of <2 between model AICc values indicated that models were not significantly different (Burnham & Anderson, 2002). Interactions between predictor variables were tested for and removed if non-significant. Specific considerations made during analyses of each carbon pool are outlined in the following sections.

Above- and belowground biomass

Total plot-level aboveground biomass, basal area, community-weighted mean wood density and carbon stocks, and belowground root biomass and carbon stocks were modelled using GLMs with a normal distribution. Each of these variables were modelled as a response to forest stand age, and plot-level mean available phosphorus and plot-level mean percentage nitrogen (0-100 cms; Table S2.1). As these were plot-level analyses, fitting random effects for 'land use' and 'substrate geology' was not possible due to over-parameterising models.

Necromass

Transect-level carbon stock estimates were modelled using GLMMs, fitting 'plot' as a random effect to account for potential pseudoreplication of transect-level data. Necromass diameter class (<20 cm or >20 cm) and forest age were fitted with an interaction term, and included alongside necromass abundance and volume in analyses of carbon stocks. Necromass carbon stocks and volume were modelled using a Gamma distribution, and necromass abundance modelled using a Poisson distribution (Table S2.1).

Soil

Soil carbon stock estimates from each sample were modelled using GLMMs, fitting 'substrate geology' and 'land use', as well as 'plot' and 'sampling point' as random effects to account for plot-level variation in topography and wider landscape characteristics. Soil carbon stocks, percentage carbon, percentage nitrogen, available phosphorus, and the C:N ratio were modelled with soil depth and forest stand age (Table S2.1). Percentage carbon and percentage nitrogen were modelled using a Beta distribution and carbon stocks, C:N ratio and available phosphorus were modelled using a Gamma distribution. Available P was not included as a predictor variable for soil carbon stocks because available P data were only available for 0-10cm and 10-20cm depths. However we assessed the relationship between soil carbon stocks and available P for the top two soil depths and found no significant relationship ($z = -0.86$, $P=0.39$).

310 # 3. RESULTS

311 ## 3.1 Carbon stocks and contributions to total forest carbon

312 Total carbon stocks ranged from ~245 – 298 Mg C ha^{-1} across the chronosequence (Table 1). Soil
313 carbon constituted the greatest percentage of total forest carbon stocks (52 – 70 %) followed by
314 aboveground biomass (24 – 39 %; Table 1).

315

316 **Table 1:** Total forest carbon and mean carbon stocks for above- and belowground carbon
317 pools, across secondary tropical forest stands of 40-120 years; 95 % confidence intervals
318 are presented in brackets. The percentage contributions to total forest carbon stocks are
319 presented in italics.
320

Forest age (years)		40	60	90	120
Mean carbon stocks (Mg ha^{-1})	Aboveground biomass	61.35 (59.82-62.88) *24.37*	75.11 (73.50-76.71) *25.21*	96.25 (85.60-106.91) *39.23*	96.86 (87.76-106.00) *32.86*
	Necromass	1.72 (1.51-1.93) *0.68*	2.42 (1.99-2.85) *0.81*	3.63 (2.46-4.53) *1.37*	3.34 (2.62-4.06) *1.13*
	Belowground biomass	12.48 (11.50-13.46) *4.96*	14.75 (13.86-15.64) *4.95*	17.45 (17.23-17.66) *7.11*	18.96 (13.06-24.86) *6.43*
	Soil (0-100 cm)	176.22 (172.2-180.30) *69.99*	205.70 (200.4-211.00) *69.03*	128.04 (118.20-123.90) *52.18*	175.60 (172.40-178.80) *59.57*
	Total	251.77 (245.03-258.57)	297.98 (289.75-306.20)	245.37 (223.49-253.00)	294.76 (275.84-313.72)

321

322 3.2 Above- and belowground biomass and carbon stocks

323 Mean carbon stocks held in aboveground biomass of trees ≥10 cm DBH ranged from ~61 – 97 Mg
324 ha^{-1}. The total basal area of trees and aboveground carbon stocks significantly increased with forest
325 age; however, the community-weighted mean wood density of forest stands showed no significant
326 relationship with forest age (Fig. 2b; Table 2). Soil nutrients (% N and available P; Table 2) were not
327 significant predictors of basal area, aboveground carbon stocks, nor community-weighted mean wood
328 density, and were not related to forest age (Table 2). Estimated carbon stocks in root biomass ranged
329 from ~12-19 Mg C ha^{-1} and significantly increased with forest age, but not soil nutrients (Table 2).
330

Table 2: Coefficient estimates for fixed effects within best-fit generalised linear models (GLMs) and generalised linear mixed-effects models (GLMMs). Marginal R^2 (R^2_m) represents the degree of model fit contributed by the fixed effects alone, while the conditional R^2 (R^2_c) shows the degree of model fit considering both random and fixed effects included within models (computed using 'r.squaredGLMM' in the 'MuMin' R package; Barton 2016). R^2 values were not computed for models using a Beta distribution (see Table S2.1).

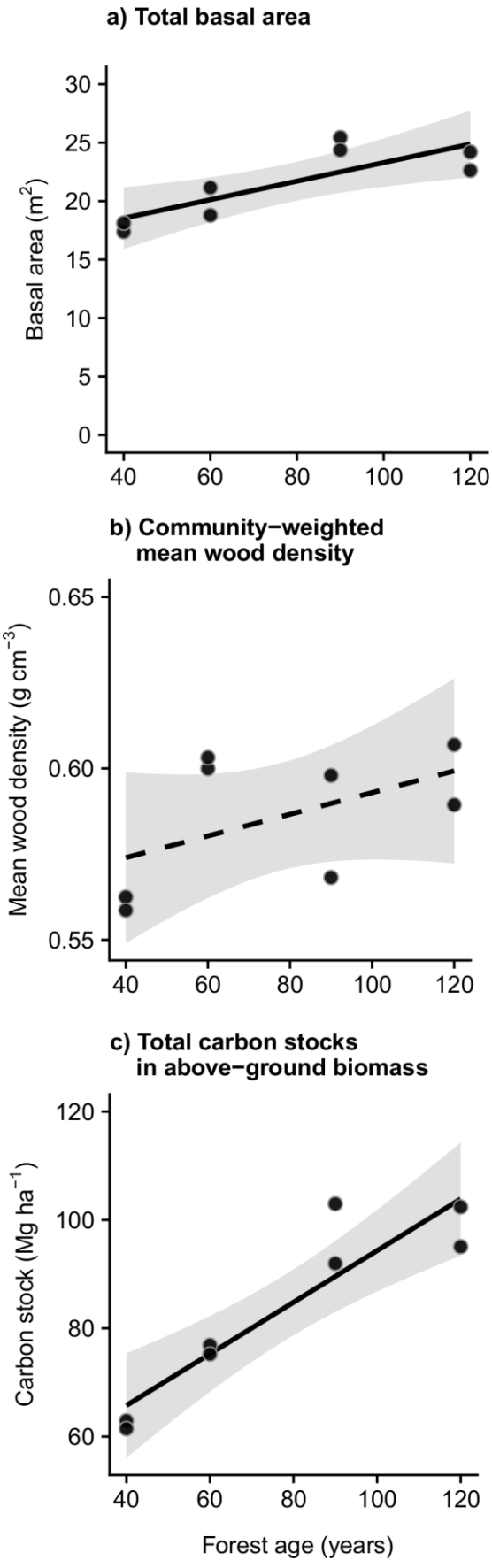
*t-value computed rather than z-value.

Carbon pool	Variable	Fixed effects	Estimate	Std. error	z-value	R^2_m	R^2_c
Aboveground biomass	C stock (Mg ha^{-1})*	Intercept	82.39	2.57	32.02	0.81	-
		Forest age (years)	30.06	5.5	5.46		
	Basal area (m^2)*	Intercept	21.45	0.71	30.14	0.6	-
		Forest age (years)	5	1.52	3.26		
	Community-weighted mean wood density (g cm^{-3})*	Intercept	0.59	0.006	91.64	0.26	-
		Forest age (years)	0.02	0.01	1.55		
Necromass	C stock (Mg ha^{-1}) (considering fallen necromass only)	Intercept	-0.36	0.08	-4.45	0.83	-
		Forest age (years)	-0.30	0.16	-1.86		
		Volume	1.61	0.16	9.81		
		Abundance	0.52	0.14	3.80		
		Forest age : diameter >20 cm	0.61	0.24	2.54		
	Volume (m^3 ha^{-1})	Intercept	1.91	0.16	12.18	0.36	-
		Diameter class	1.15	0.22	5.21		
		Abundance	0.94	0.25	3.75		
	Abundance	Intercept	1.46	0.08	18.64	0.04	-
		Forest age (years)	-0.43	0.15	-2.79		
		Diameter class	0.58	0.13	-4.4		
		Forest age : > 20 cm	0.95	0.26	3.66		
Belowground biomass	C stock (Mg ha^{-1})*	Intercept	19.53	0.56	34.55	0.86	-
		Forest age (years)	7.88	1.30	6.05		
Soil	C stock (Mg ha^{-1})	Intercept	3.76	0.06	57.99	0.45	0.57
		% N	0.69	0.05	13.60		
	% C	Intercept	-3.36	0.05	-61.80	-	-
		% N	0.84	0.05	16.26		
		Depth 10-20 cm	-0.22	0.04	-5.00		
		20-50 cm	-0.88	0.07	-12.49		

		50-100 cm	-1.49	0.10	-15.16		
	% N	Intercept	-0.17	0.11	-1.58	-	-
		Soil depth: 10-20 cm	-0.75	0.07	-10.00		
		20-50 cm	-1.33	0.10	-13.87		
		50-100 cm	-1.80	0.11	-16.27		
	Available P (mg kg^{-1})	Intercept	1.58	0.23	6.73	0.08	0.17
		% N	0.21	0.31	0.67		
		Soil depth: 10-20cm	-0.81	0.28	-2.9		
	C:N	Intercept	2.41	0.06	37.36	0.51	0.60
		Soil depth: 10-20 cm	-0.13	0.06	-2.34		
		20-50 cm	-0.49	0.06	-7.66		
		50-100 cm	-0.99	0.07	-15.23		

3.3 Necromass volume, abundance and carbon stocks

Across the chronosequence, total necromass carbon stocks ranged from 1.72 – 3.63 Mg ha^{-1}. Stand age alone was not a significant predictor of necromass carbon stocks. However, there was a significant interaction between stand age and necromass diameter, such that carbon stocks were increasingly held in larger (>20 cm) deadwood in older secondary forests >90 years. Larger deadwood made a greater contribution to the total necromass volume in older stands, while the contribution of smaller deadwood (10-20 cm) decreased with stand age (Fig. 3; Table 2). Necromass carbon stocks significantly increased with higher values of necromass volume and abundance (Table 2). Overall, necromass carbon stocks were predominantly contained within fallen deadwood (~80-95%) compared to standing deadwood.


a) Total basal area
Basal area (m2)
30
25
20
15
10
5
0
40
60
80
100
120
b) Community−weighted mean wood density
Mean wood density (g cm−3)
0.65
0.60
0.55
40
60
80
100
120
c) Total carbon stocks in above−ground biomass
Carbon stock (Mg ha−1)
120
100
80
60
40
60
80
100
120
Forest age (years)

349

350

Fig. 2: Relationship between total basal area, community-weighted mean wood density, and aboveground biomass carbon stocks for trees ≥10 cm DBH across eight 1-ha forest plots of varying age. Solid regression lines indicate a significant relationship, with 95 % confidence intervals represented by grey shading; dashed lines indicate a non-significant trend (Table 2).

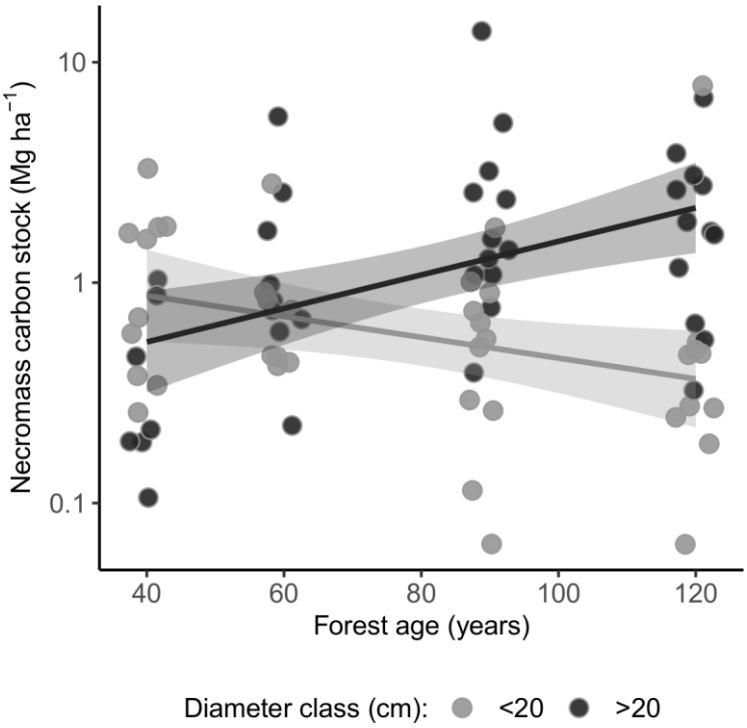


Fig. 3: Necromass carbon stocks in large (>20 cm diameter) and small (10-20cm diameter) deadwood in secondary forest stands of 40-120 years. Predicted values and 95 % confidence intervals are plotted as solid lines and grey shading respectively. A $\log_{10}$ scale is used on the y-axis to aid visual clarity. Data represent fallen necromass only (Table 2).

3.4 Soil carbon stocks

Mean total soil carbon stocks ranged from ~176 – 206 Mg C ha^{-1} in each stand across the chronosequence (Table 1). The concentration of soil carbon (% C) and total soil carbon stocks (Mg C ha^{-1}) did not vary significantly across forest ages (Fig. S2.1; Table 2). Percentage C significantly declined with depth, but this was not reflected in carbon stocks due to changes in soil bulk density (SI1), and carbon stocks did not significantly change with soil depth (Fig.

S2.1; Table S2.3). Soil carbon stocks were significantly positively related to % N (Fig. 4; Table 2), but were not related to available P or aboveground biomass (Table 2). Forest stand age did not predict % N in soils, nor available P (Table 2; Table S2.2), however % N decreased with soil depth, as did the C:N ratio and available P (Fig. S2.2; Table 2). Prior land use and substrate geology explained no variation in soil carbon or nutrient concentrations (Table S2.1).

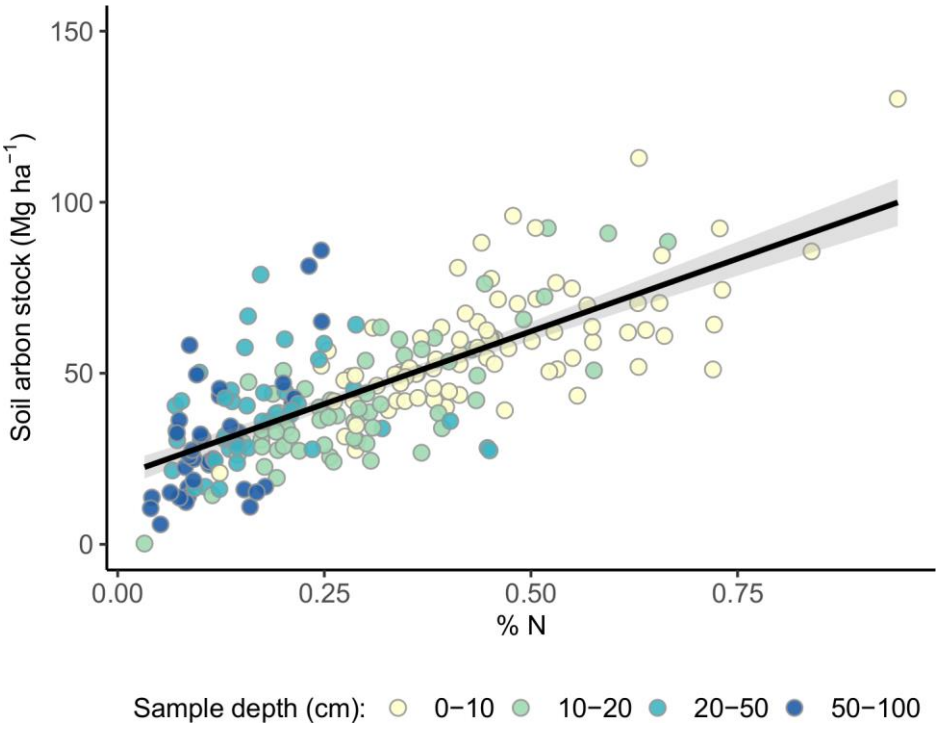


Fig. 4: Relationship between soil carbon stocks and soil N concentration (% N) within soils 0-100 cm. The black line corresponds to predicted values, with 95 % confidence intervals indicated by grey shading. Points relate to individual sampling points.

3.5 Landscape-scale context of the 40-120 year chronosequence carbon pools

Aboveground biomass carbon stocks in our 40-year-old forest stands were within the range of values from nearby young secondary forests (5-15 years; Fig. 5). Estimated aboveground carbon stocks in old-growth forest were slightly higher than those of our 120-year-old stands, indicating that aboveground biomass may still be on a trajectory of recovery beyond 120 years (Fig. 5). Conversely, our chronosequence soil carbon stock estimates were significantly higher

than those for young secondary forests, but confidence intervals overlapped with those for old-growth forests indicating that our soil carbon estimates were within the range of variation for old-growth forests (Fig. 5). When viewed at the landscape scale, aboveground carbon stocks appear to increase with forest age, whereas soil carbon stocks do not show a clear trajectory of change in relation to forest age.

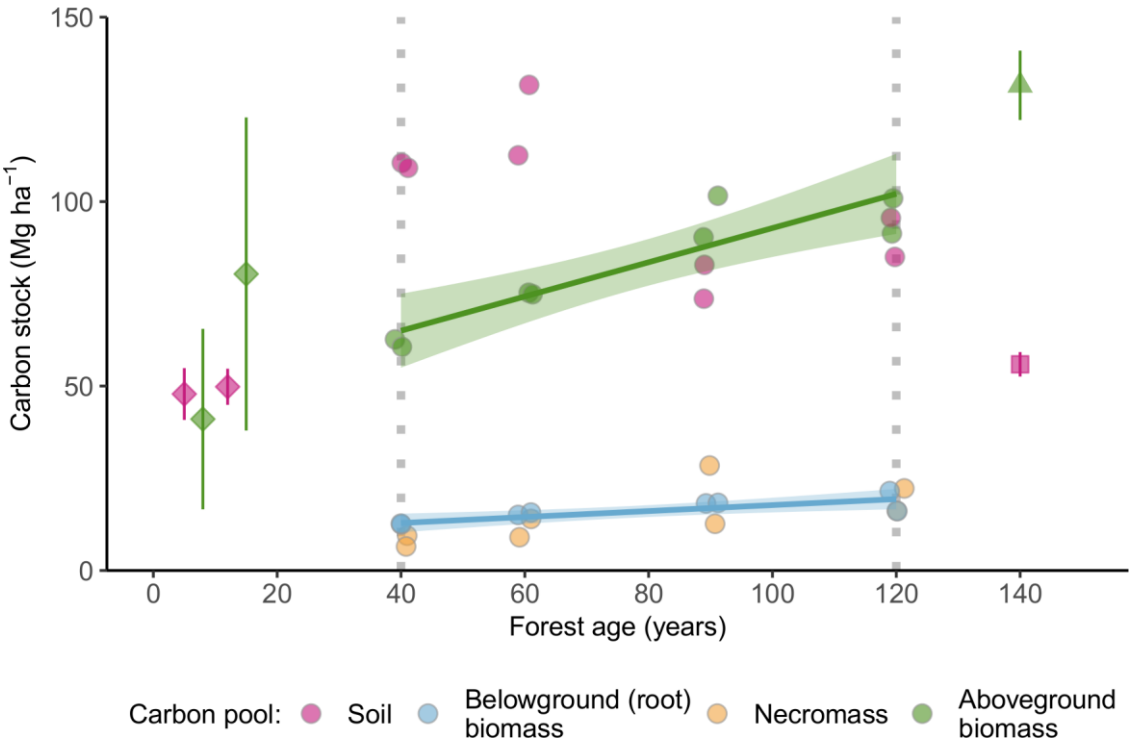


Fig. 5: Overview of carbon stocks at the landscape-scale. Carbon stock estimates from the eight 1-ha chronosequence plots in this study are shown within the grey dotted boundaries, with significant relationships between carbon pools and forest age denoted by solid regression lines; 95 % confidence intervals are shown as shaded areas. Additionally, soil carbon and aboveground carbon stocks are reported from nearby Agua Salud for young secondary forests 5-15 years old (diamonds; Neumann-Cosel et al., 2011). Soil carbon stocks (square; Grimm et al. (2008)) and aboveground carbon stocks (triangle; Chave et al., 2003)) are plotted for old-growth forest on BCI (Fig. 1); an 95 % confidence intervals are indicated by vertical bars. Points are coloured by carbon pool.

Only soil carbon stocks 0-20 cm in depth are reported to allow comparison between studies.

4. DISCUSSION

We found that above- and belowground carbon stocks are decoupled in their relationships with forest stand age and soil nutrient status: carbon stocks in aboveground biomass increased with secondary forest age but showed no relationship with soil nutrients, while conversely, soil carbon stocks were positively related to soil nutrients (specifically % N) but not stand age. The soil carbon pool contributed 52 – 70 % of total forest carbon, and when viewed at the landscape scale, 40-year-old secondary forests had attained soil carbon stocks equivalent to those reported for old-growth forests. Aboveground biomass contributed 24 - 39 % of total forest carbon, and after 100 years of regrowth, was close to recovery towards old-growth forest biomass and may still be on a trajectory of recovery beyond 120 years.

4.1 Effect of forest age on carbon stocks

As in other studies, we found that over tropical forest succession, aboveground and root biomass carbon stocks increased predictably and tracked forest age (Powers & Marín-Spiotta, 2017). However, as root biomass is estimated from aboveground biomass in our study, there remains some uncertainty regarding carbon stocks in this carbon pool (Sierra et al., 2007). Community-weighted mean wood density showed no relationship with stand age and was slightly higher than old-growth forests on BCI (basal-area-weighted mean wood density = 0.51 ± 0.16; Muller-Landau, 2004), indicating that our secondary forest stands have recovered this key functional trait during forest regeneration, in contrast to recent findings from Amazonian secondary forests (Berenguer et al., 2018). We found no relationship between forest stand age and necromass volume, abundance, and carbon stocks. However, both the volume and carbon stock of necromass was increasingly contributed by larger diameter (>20 cm) deadwood in older forest stands >90 years (DeWalt, Maliakal, & Denslow, 2003). The decomposition rate for larger diameter necromass is lower than for small necromass; deadwood

of ~20 cm diameter takes an estimated 18 years to lose 95 % of its mass at a rate of 0.19 $year^{-1}$ (Chambers, Higuchi, Schimel, Ferreira, & Melack, 2000). Thus, the increasing abundance of large necromass in older secondary forests suggests that the necromass carbon pool in secondary forests >90 years could be more stable and retain carbon for longer than in younger forests (Carey, Brown, Gillespie, & Lugo, 1994).

Patterns in soil carbon dynamics are highly variable (Powers & Marín-Spiotta, 2017). Early studies assumed that patterns of soil carbon would mimic those of aboveground biomass (Detwiler, 1986), but results from field studies are inconsistent, with studies reporting increased, decreased or unchanged soil carbon stocks across tropical secondary forest succession (Powers & Marín-Spiotta, 2017). Secondary forest stand age did not predict soil carbon stocks in our study, and the confidence intervals of our 0-10cm and 10-20cm soil carbon stocks overlapped with those reported for a comparable study of soil carbon (i.e. 0-10 cm and 10-20 cm soil layers) in old-growth forests on BCI (Grimm et al., 2008), indicating that our soil carbon stocks were similar to this old-growth forest stand. When using comparable soil data (i.e., the 0-10 cm and 10-20 cm soil layers), soils underlying our 40-year stands held significantly more carbon than reported for nearby young secondary forests (Neumann-Cosel et al., 2011) pointing towards rapid accumulation of soil carbon within the first 40 years of secondary forest regeneration (Poorter et al., 2016; Powers, 2004). Some evidence suggests that stand age may be most influential on soil carbon stock recovery during the first 10-30 years of succession, along with additional factors that we could not include in analyses (such as composition of the regenerating forest; Batterman et al., 2013; Berenguer et al., 2014). We found that prior land use and substrate geology explained no variation in soil carbon stocks. The implications of complex land use histories and underlying geology for biogeochemical cycles across secondary forest regeneration are thoroughly reviewed in Powers & Marín-Spiotta (2017).

4.2 Effect of soil nutrients on carbon stocks

Across the chronosequence, aboveground biomass accumulation was not related to soil nutrients (% N and available P). A lack of relationship between aboveground biomass recovery and broad-scale soil nutrient availability (CEC) has been shown in a pan-Neotropical analysis of secondary forest biomass accumulation (Poorter et al., 2016). However, at finer spatial scales, soil nutrients have been shown to be an important limiting factor for biomass accumulation in trees <10 cm DBH and root biomass (Powers & Peréz-Aviles, 2013; Wright et al., 2011). Thus, soil nutrient status could be important in determining the trajectory of biomass accumulation in younger secondary forest stands <40 years.

Carbon and nitrogen are tightly coupled in tropical forest soils due to stoichiometric relationships in both vegetation and soil (Yang & Luo, 2011). Our finding that soil nitrogen concentration (% N) is the strongest correlate of soil carbon stocks across the chronosequence aligns with other studies of C and N accumulation across regenerating forests (Li, Niu, & Luo, 2012; Yang & Luo, 2011). Both % C and % N significantly declined with soil depth; however, when integrated with soil bulk density data, this pattern did not translate to a reduction in soil carbon stocks with soil depth (Grimm et al., 2008). Thus, we highlight the necessity of correcting % C data using soil bulk density when estimating soil carbon stocks (Li et al., 2012). That carbon stocks did not decline with soil depth highlights the importance of deeper tropical soils for carbon storage, and suggests that estimates of the contribution of soil carbon to total forest carbon stocks are improved by including carbon stock estimates from deeper soils (Jobbagy & Jackson, 2000; Ngo et al., 2013).

4.3 Contribution of different carbon pools to total forest carbon stocks at local and landscape scales

When integrated with additional landscape-scale data on aboveground biomass carbon stocks, our data show a trajectory of aboveground biomass accumulation towards that of old-growth forests (Fig. 5; Mascaro et al., 2011; Mascaro, Asner, Dent, DeWalt, & Denslow, 2012). However, carbon in aboveground biomass of our oldest secondary forest sites (120 years) was lower than nearby old-growth forest, suggesting that biomass recovery may continue past 120 years. Across our sites, total carbon stocks held in aboveground biomass ranged from ~61 – 97 Mg ha^{-1}, which is lower than

predicted for similar-aged secondary forests in a recent pan-Neotropical analysis, likely due to characteristics of our study area such as the pronounced dry season or differences in tree community composition (Poorter et al., 2016).

In contrast to aboveground biomass, soil carbon stocks were variable across the wider landscape, but our data suggest that soil carbon has recovered to old-growth levels within 40 years of forest regrowth following agricultural abandonment (Powers, 2004; Powers & Marín-Spiotta, 2017). Our study showed that soil contributed 52 - 70 % of total forest carbon stocks, which contrasts with other estimates of carbon pool contributions, whereby aboveground biomass contributed the greatest proportion (56 %) of total forest carbon stocks compared to 32 % in soil (Pan et al., 2011). However, this difference is likely due to our soil carbon estimates incorporating deeper soils (0-100 cm).

The necromass carbon pool held 1.7 - 3.6 Mg C ha^{-1}, similar to other Neotropical forests (Fonseca, Benayas, & Alice, 2011; Sierra et al., 2007) and for 20-100 year secondary forests pan-tropically (~5 Mg C ha^{-1}; Anderson-Teixeira et al., 2016). Our necromass carbon stock estimates are also similar to those in old growth forests on BCI (4.6 [3.1-6.39] Mg C ha^{-1}; H. Muller-Landau, pers. comm.). However, the necromass carbon stock estimates from our 120-year-old stands and the BCI 50-ha plot are lower than for other old-growth tropical forests pan-tropically (~17 Mg C ha^{-1}; Anderson-Teixeira et al., 2016).

4.4 Implications for global carbon modelling

Above-and belowground carbon stocks in this system appear to be decoupled. Aboveground carbon accumulates over time due to inputs from NPP, unless there are substantial disturbances such as deforestation (Powers & Marín-Spiotta, 2017). In contrast, soil carbon is influenced both by NPP, soil micro-organisms and abiotic factors such as geology, climate and topography that can affect soil nutrients (Jackson et al., 2017). Given that soil contributed the greatest proportion of total secondary forest carbon in our study, we emphasise that global models of the value of secondary forests for

carbon accumulation and storage must include soil carbon estimates. Moreover, our study shows that models of carbon accumulation through secondary forest regeneration can be better calibrated by including site-level data on soil nutrient availability, alongside forest stand age, leading to improved predictive power of large-scale models of secondary forest carbon accumulation (Chazdon et al., 2016; Powers & Marín-Spiotta, 2017). Our study demonstrates the importance of detailed soil nutrient and carbon stock information for parameterising global models of the significant contribution increasing secondary tropical forest cover can make to climate change mitigation.

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